



A null biogeographic model for quantifying the role of dispersal in shaping taxonomic richness and similarity patterns

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Diversity patterns in the fossil record are often interpreted as functions of only origination and extinction, while taxonomic dispersal among regions is rarely considered. We present a null biogeographic model of global diversity, that calculates taxonomic richness (S) and similarity (J), as measured by the Jaccard Coefficient. The model contains three regions, each initially containing a unique set of taxa. At each time step, each taxon is randomly allowed to go extinct, create a new taxon, disperse or remain unchanged. At the end of each time step, global S and mean global J are calculated. The probabilities for origination and extinction are set to be equal and the model was run with origination/extinction and dispersal probabilities that spanned over four orders of magnitude.

The model has two significant results. (1) If the probability of dispersal is sufficiently large relative to origination/extinction, regional and global richness increase exponentially. For non-negligible probabilities of origination, the combined effect of dispersal and origination exceeds the effect of extinction, causing the exponential increase in diversity. (2) If richness increases, global mean J will reach equilibrium (J_{eq}). When plotted against the ratio of dispersal probability to origination/extinction probability, J_{eq} follows a sigmoidal curve.

This null biogeographic model is useful for predicting dispersal probabilities in the fossil record when origination and extinction probabilities are known. Taxonomic dispersal among regions has the potential to play a significant role in shaping diversity trends, and should be considered when analysing Phanerozoic diversity trends.

Might machaeridians be molluscs?

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Machaeridians were elongate, slug- or worm-like organisms with an external skeleton of imbricating calcite plates (sclerites). Known only from Palaeozoic marine environments, three groups are recognized—plumulitids, turrilepadids and lepidocoleids—but their zoological affinities are enigmatic. Withers (1926) recognized that they formed a monophyletic group, but was uncertain of their systematic position. He did note similarities between the optical properties of machaeridian sclerites and echinoderm ossicles, leading many later workers to interpret machaeridians as aberrant members of the Echinodermata. However, Bengtson (1978) showed this to be erroneous, and subsequent studies have suggested variously that machaeridians are most closely related to arthropods, annelids or molluscs. Using specimens from the Much Wenlock Limestone Formation (Silurian) of England, new information is presented here that indicates machaeridians are molluscs, probably the sister-group of Polyplacophora + Conchifera.



Bengtson, S. 1978. The Machaeridia – a square peg in a pentagonal hole.

Thalassia Jugoslavica, 12, 1–10.

Withers, T. H. 1926. *Catalogue of the Machaeridia (Turrilepas and its allies) in the Department of Geology*. British Museum (Natural History), London, XV+99 pp.

Echinoderm Palaeoecology from fragments: reconstructing salinity and substrate controlled faunas in the British Middle Jurassic

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Research using bulk sampled sediments (of typically 10–40kg) from across the British Middle Jurassic (Bathonian), where the full spectrum of marine and marginal marine environments are represented, has demonstrated a distinct ecological zonation pattern in the crinoid groups characterised by at least two genera.

This research has been taken a stage further with its application to three more echinoderm groups (echinoids, asteroids and ophiuroids). Previously it was noted that lack of homology in the ossicles made identification beyond family level problematic; however, examination of complete specimens in museum collections has allowed the recognition of diagnostic ossicles that can identify tests, spines and marginal plates to generic level.

Results indicate a marked facies control on the distribution of groups influenced by factors including substrate and salinity. Groups such as echinoids inhabit ecosystems defined by facies belts; for example, *Hemipedinia* inhabits normal marine settings, *Hemicidaris* is found in open shelf areas and *Acrosalenia* is found in lagoonal and restricted conditions. Such results are also mirrored in the asteroid and ophiuroid data.

This new data, combined with the previous findings on crinoid groups, has allowed the construction of a model for echinoderm palaeoecology across marginal marine environments. The application of this model to marine environments outside the British Jurassic, such as the Middle Jurassic of France and the Western interior, USA, has demonstrated that factors such as substrate and marine connection have a greater bias than geographical and stratigraphic controls.

Early eukaryotes in Paleoproterozoic and Mesoproterozoic oceans

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Biomarker molecular fossils in 2770 Ma shales suggest that the Eucarya diverged from other principal domains early in Earth history. Nonetheless, at present, the oldest fossils



that can be assigned to an extant eukaryotic clade are filamentous red algae preserved in *ca.* 1200 Ma cherts from Arctic Canada. Between these records lies a rich assortment of potentially protistan microfossils. New microscopic study of late Paleoproterozoic shales from China (1800–1625 Ma Chuanlinggou Formation) and Australia (1650 Ma Mallapunyah Fm) permits the significant extension of the stratigraphic range of fossil evidence for early eukaryotes. Combined light microscopy, scanning electron microscopy, and transmission electron microscopy on fossils from the 1500–1400 Ma Roper Group, Australia, and broadly coeval rocks from China show that these intermediate assemblages do indeed include a moderate diversity of eukaryotic remains, although the observed diversity remains well below Neoproterozoic levels. In particular, preserved cell wall ultrastructure, observed using transmission electron microscopy (TEM), can help to bridge the current stratigraphic gap between the unambiguous eukaryotic morphologies of mid-Proterozoic assemblages and molecular biomarkers in much older rocks. Ongoing microchemical analyses (Micro-FTIR spectroscopy, Laser micro-Raman spectroscopy and Laser micro-pyrolysis-GC/MS) of individual microfossil walls may help us to place firmer constraints on phylogenetic interpretation.

Homology, shape and morphometric analysis of the conodont skeleton

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Conodonts possess an exceptionally good fossil record and occupy a key phylogenetic position within the vertebrate clade. Consequently, they represent an invaluable tool for understanding both evolutionary patterns and the acquisition of vertebrate characters. Correct identification of homology is vital in exploiting this potential. However, as with most vertebrates, conodonts are rarely preserved as articulated skeletons, where homology can be determined directly from topological relationships. Traditionally homology has therefore been identified exclusively through qualitative description of the morphology of disarticulated elements. Yet hypotheses of homology based on articulated skeletons may contradict those derived from the morphology of isolated elements alone. Here, quantitative morphometric analysis of both skeletons and isolated elements is used to determine rigorously whether element morphology is an accurate guide to element homology.

A new Upper Permian flora from the Middle East with typical Triassic Gondwana elements

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Several species of *Dicroidium* are described from the Um Irna Formation (Upper Permian) of the Dead Sea region, Jordan. Plant remains are preserved as compressions with excellent cuticles. It is the earliest unequivocal record of *Dicroidium*, a genus that is typical for the Triassic of Gondwana and the northernmost occurrence of this genus that apparently originated in the Late Permian in the palaeotropics. Middle and Late Permian floras from the Arabian Peninsula show a remarkable mixture of elements from different floral provinces, *i.e.* Euramerica, Cathaysia and Gondwana. The climatic amelioration that has been reported for the Early Triassic of the Gondwana apparently enabled *Dicroidium* to migrate southward and finally colonize the entire Gondwana region. *Dicroidium* is one of the very few megaplant genera that was not affected by the biotic crisis at the Permian-Triassic transition.

Discovery of Famennian and Early Carboniferous trilobite larvae: implications for the systematics and the evolutionary history of proetoids

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New silicified material from the Middle Famennian of Morocco, the Late Famennian of Germany, and the Early Carboniferous of France substantially increase our knowledge of proetoid larvae. Both anaprotaspides and metaprotaspides illustrate that proetoid trilobites possess a unique early ontogeny, remaining highly conservative from the Ordovician to the Early Carboniferous. Accordingly, they support the view that Proetida may be composed of two different clades. The new data also enable the evolution of anaprotaspis size in proetoids from the Ordovician to the Lower Carboniferous to be broadly depicted. In particular, two marked increases of larval sizes are recognised. The first one may have occurred around the Silurian/Devonian boundary, but its potential implication on proetoid evolutionary history is unknown. On the other hand, the substantial sizes reached by Late Famennian and Early Carboniferous anaprotaspides suggest the acquisition of an extended planktonic period in the early ontogeny of proetoids. The possible implications of this developmental strategy on the survivorship of these trilobites during the end Devonian Hangenberg biocrisis or, alternatively, on the colonization of deep water benthic habitats, are discussed.

Towards the development of a Palaeo UV-B proxy from fossil land plants

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Changes in atmospheric oxygen, major volcanic eruptions and impact events have the potential to induce short- and long-term changes to the stratospheric ozone layer. However, detecting the interaction between these events and the expected increase in terrestrial UV-B flux has proved elusive.